Diets of deep-sea brachyuran crabs in the Western Mediterranean Sea

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Abstract. This study examines the feeding habits of *Paromola cuvieri* (Risso, 1816) and *Geryon longipes* A. Milne Edwards, 1881, the only two common deep-sea brachyuran crabs inhabiting the bathyal mud assemblages in the Catalan Sea (Western Mediterranean). Samples were obtained by bottom trawls at depths between 360 and 1871 m during 1983 to 1992. Both species had highly diverse diets, but very low feeding activity, as reflected by the high proportion of empty stomachs. Both characteristics may be important factors enabling deep-sea crabs to adapt to bathyal zones, where trophic resources are scarce. The most important food items found in *P. cuvieri* were fish remains (teleost, sharks) and benthic decapods (*Monodaeus couchii, Munida tenuimana*). Scavenging activity plays an important role in this species. The diet of *G. longipes* included a broad range of benthic invertebrates. In the upper middle slope, the bivalve *Abra longicallus*, decapods (*Calocaris macandreae* and *Monodaeus couchii*), echinoderms and polychaetes were the dominant prey, with epibenthic peracarids as a secondary resource. On the lower middle slope, the incidence of decapod crustaceans (*C. macandreae, Pontophilus norvegicus*) and peracarids in the diet declined. Small macrobenthic prey (glycerids, cumaceans or amphipods) were rare in the diet of both species, in accordance with the large size of the crab specimens studied. The absence of preferred prey items and the lack of food items of an optimum size on the lower slope may contribute to the progressive decline in abundance of *P. cuvieri* and *G. longipes* with increasing depth.

Introduction

Brachyuran crabs of families such as Lithodidae, Homolidae or Geryonidae are characteristic of bathyal oceanic communities (Lagardère 1977, Wenner and Boesch 1979, Haedrich et al. 1980, Manning and Holthuis 1981, 1989). In deep-bathyal Mediterranean mud assemblages (cf.

Pérès 1985), the homolid *Paromola cuvieri* (Risso, 1816) and the geryonid *Geryon longipes* A. Milne Edwards, 1881 are the only two large crab species that occur with relatively high frequency and abundance (Abelló et al. 1988, Cartes and Sardà 1992).

Paromola cuvieri is distributed between 150 and 600 m in the upper and middle slope in the Western Mediterranean (Mori 1986, Abelló et al. 1988). Along the deep slope of the Catalan Sea this species is found between 360 and 1165 m (Cartes 1993a), but is more abundant in the upper middle slope (550 to 750 m). *P. cuvieri* is relatively frequent in soft-bottom communities, although its density is always very low, being usually restricted to 1 individual per haul. This species prefers intermixed bathyal mud and emerging rocky substrates (Pérès 1985) that are difficult to sample with bottom trawls.

The geryonid crab *Geryon longipes* is characteristic of middle-slope communities (Abelló et al. 1988, Cartes 1991). In the present study, the species was found between 610 and 1871 m, being abundant only between 610 and 1322 m. Its density decreased drastically below 1300 m depth (Cartes and Sardà 1992). *G. longipes* is captured regularly during red shrimp (*Aristeus antennatus*) fishery (Relini-Orsi and Würtz 1977).

Although natural diets have been established for various species of shallow-water crabs and lobsters (e.g. Williams 1982, Brêthes et al. 1984, Elner and Campbell 1987, Wassenberg and Hill 1987), little information is available on the feeding habits of deep-sea crabs, particularly below 1000 m. The feeding habits of *Paromola cuvieri* have been studied only by Mori (1986) in the Ligurian Sea, where its diet consists of brachyuran and natantian decapods, bivalves and fish remains, a highly diversified diet. The diet of *Geryon longipes* includes a great variety of benthic invertebrates (Lagardère 1977, Relini Orsi and Mori 1977). Lagardère described *G. longipes* as an active scavenger, feeding primarily on fish remains, for which the crab actively searches. In contrast, fishes identified in the diet of *G. longipes* in the Ligurian Sea seemed to have been ingested by active predation rather than by scavenging (cf. Relini Orsi and Mori 1977).

Table 1. *Paromola cuvieri* and *Geryon longipes*. Catch data

| Sample No.	Date		Depth (m)	Number of specimen of:	
				P. cuvieri	*G. longipes*
1	24 Oct.	1988	626– 669	2	5
2	13 Jul.	1989	650– 700	0	17
3	13 Jul.	1989	640– 700	0	4
4	14 Jul.	1989	640– 660	0	7
5	14 Jul.	1989	710– 730	0	15
6	14 Jul.	1989	610– 640	0	17
7	5 Nov.	1990	550– 595	2	10
8	5 Nov.	1990	569– 610	2	14
9	1983–1984		1127–1871	0	8
10	Jul.	1987	1270–1420	0	9
11	10 Jul.	1988	1062–1069	0	15
12	Jul.	1988	908–1149	0	11
13	Oct.	1988	861–1049	2	12
14	Oct.	1988	1050–1149	0	13
15	Oct.	1988	1150–1249	0	5
16	Oct.	1988	1247–1795	0	7
17	16 Oct.	1989	862– 989	1	12
	11 Dec.	1990	365– 390	3	0
	5 Feb.	1991	360– 400	2	0
	Apr.	1991	620– 629	4	0
	7 Apr.	1992	375– 420	1	0
	26 May	1992	873– 865	0	1
	Nov.	1992	365– 530	4	0

The present paper examines the feeding habits of the only two common deep-sea brachyuran crabs dwelling on the Catalan Sea slope, and relates them to the bathymetric distribution and abundance of each crab species and with general changes in the food resources available in the deep-bathyal Mediterranean environment.

Materials and methods

All material was collected by bottom trawls (an OTSB-14 and commercial trawls) in the Catalan Sea area (Fig. 1) during 1983 to 1992. A total of 40 specimens of *Paromola cuvieri* and 325 specimens of *Geryon longipes* were studied. *P. cuvieri* specimens were collected in hauls between 360 and 1165 m and *G. longipes* between 610 and 1871 m (Table 1). Cephalothorax length (CL) was measured for each specimen. All specimens were preserved in 70° alcohol immediately after capture.

The stomach fullness (*f*) of each specimen was recorded; foreguts for which *f* was <20% were classified as empty, those for which *f* was ≥50% were classified as full. The fullest stomachs were used to establish the diet of the crabs in order to correct for the possible underestimation of soft-prey items (siphonophores, polychaetes, sipunculans) in the diet. All these types of prey possess hard structures (setae, mandibles, muscular body walls, etc.) which have a high retention time in the foreguts (Sardà and Valladares 1990), and which were used to identify such prey items.

In all, the contents of 24 specimens of *Paromola cuvieri* (between 12.2 and 126.7 mm CL), and 171 *Geryon longipes* (between 12.9 and 63.2 mm CL) were examined to establish the composition of the diet. Large individuals predominated in these samples. In *G. longipes*, small crabs (<40 mm CL) were mainly distributed below 1000 m (Fig. 2). However, because of the low number (10) of small specimens with stomachs containing food, diet as a function of size class was not considered in the present study. The diet of *G. longipes* was examined as a function of depth: upper middle slope (550 to 750 m), lower middle slope (1000 to 1250 m), and lower slope (be-
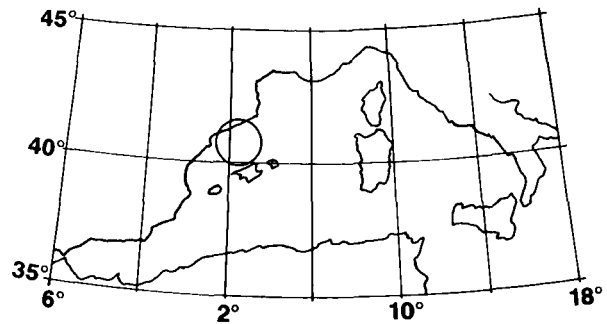

Fig. 1. Location of study area in Western Mediterranean
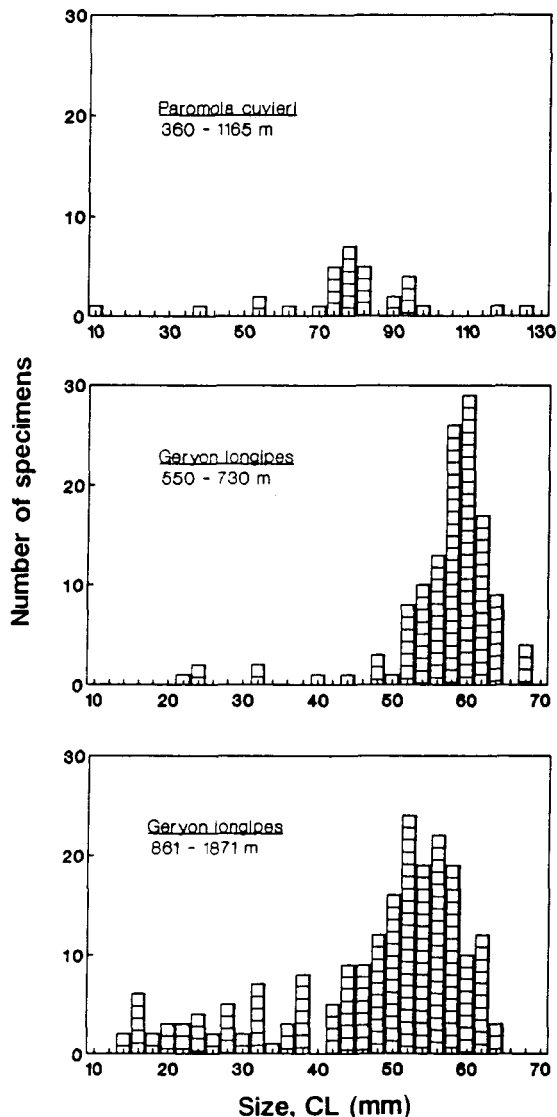
Fig. 2. *Paromola cuvieri* and *Geryon longipes*. Size-frequencies of species collected in present study

low 1300 m). These strata are characterized by different decapod assemblages (Cartes and Abelló 1992, Cartes and Sardà 1992). For the upper middle slope, the diet was also studied as a function of season (autumn and summer).

Prey were identified to species or to the lowest possible taxonomic level. The percentage frequency of occurrence (%*F*), and

Table 2. *Paromola cuvieri.* Composition (% frequency, F, and % abundance, N) of diet on middle slope. No. of stomachs examined was 24; –: Only %F was calculated for foraminiferans

Dietary component	%F	%N
Poriphera	16.7	3.7
Hydrozoa		
Stephanoscyphus spp.	4.2	0.9
Polychaeta	12.5	2.8
Crustacea		
Decapoda	45.8	13.0
Sergestidae	8.4	1.9
Calocaris macandreae	12.5	2.8
Munida tenuimana	12.5	2.8
Monodaeus quinotae	4.2	0.9
Monodaeus chouchii	20.8	4.6
Euphausiacea (M. norvegica)	8.3	1.9
Amphipoda		
Gammaridea		
Synchellidium sp.	4.2	0.9
Arrhis mediterraneus	4.2	0.9
Isopoda		
Cirolana borealis	4.2	5.6
Asellota	4.2	0.9
Unidentified Crustacea	4.2	0.9
Pycnogonida (Pallenopsis scoparial)	4.2	0.9
Mollusca		
Bivalvia	29.2	6.5
Taxodonta	4.2	0.9
Abra iongicallus	16.7	3.7
Other Bivalvia	8.3	1.9
Gastropoda	37.5	16.7
Pteropoda	29.2	9.3
Opistobranchia	4.2	0.9
Philine sp.	4.2	0.9
Cymbulia peroni	12.5	2.8
Lunata fusca	4.2	1.9
Prosobranchia (eggs capsules)	4.2	0.9
Cephalopoda	12.5	2.9
Unidentified	4.2	0.9
Echinodermata	50.0	11.1
Echinoidea	33.3	7.4
Opiuroidea	12.5	2.8
Holothuroidea		
Synaptudae	4.2	0.9
Sipunculoidea (Aspidosiphon sp.)	4.2	0.9
Chaetognata	4.2	0.9
Osteichthyes	65.5	16.7
Myctophidae	4.2	0.9
Hymenocephalus italicus	4.2	0.9
Unidentified	58.3	14.8
Chondricthyes	25.0	5.6
Others (synthetic material)	20.8	4.6
Unidentified	8.3	1.9
Foraminifera	50.0	–
Cyclammina sp.	8.3	–
Uvigerina sp.	8.3	–
Pyrgo sp.	4.2	–
Other benthic species	41.7	–
Globigerinae	20.8	–
Micromollusc remains	12.5	–
Sand	4.2	–
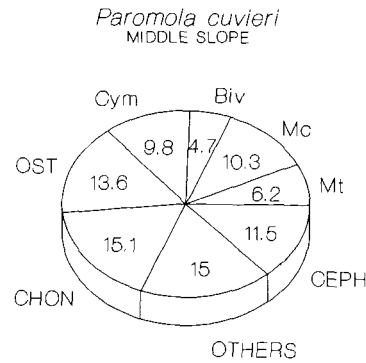
Fig. 3. *Paromola cuvieri.* Proportion (vol) of prey items in diet. Mt: *Munida tenuimana*; Mc: *Monodaeus couchi*; Biv: bivalves; Cym: *Cymbulia peroni*; CEPH: cephalopods; CHON: shark remains; OST: teleost fish remains

percentage abundance (%N) for each prey species and prey group were calculated (Hyslop 1980, Cartes and Sardà 1989), using the formulae:

$$\%F = 100 \times \text{(no. of stomachs containing a given prey item/total no. of stomachs examined)};$$

$$\%N = 100 \times \text{(no. of prey items of a given category/total no. of prey items)}.$$

Foraminiferans were not quantified in this study, and only the %F of these organisms was recorded. Percentage volume for the different prey groups was estimated by the subjective-points method (Swynnerton and Worthington 1940).

In order to reveal possible variations in the trophic habit (diet) of *Geryon longipes*, a principal-components analysis (PCA) was made. Data matrix was obtained using the abundance (%N) of each prey item (see Table 3) in each sample. Whenever possible, samples consisted of individuals collected in a single haul. Samples containing a low number of specimens (<7) were grouped by depth or season (Table 1). Trophic diversity in the diet of each species was established using the Shannon-Wiener index (Shannon and Weaver 1963). The percentage similarity used by Schoener (1970) was used to establish dietary affinities. These two indexes were calculated for each of the sample groups established.

Results

Paromola cuvieri

Although the contents of only 24 stomachs were analyzed, this number is considered sufficient to obtain a reliable estimate of this species' diet. In *Geryon longipes*, a species with a similarly diversified diet, asymptotic stabilization of the curve of cumulative trophic diversity was observed after the analysis of 20 foregut contents (Mauchline and Gordon 1985).

Fish remains, pteropod debris and echinoids predominated in the diet of *Paromola cuvieri*. Foraminiferans were present only in moderate amounts (Table 2). In terms of percentage volume (Fig. 3), the predominant food items were also shark and teleost remains, followed (in decreasing order of volume) by decapods (*Monodaeus couchii, Munida tenuimana*), *Cymbulia peroni* and non-assimilable remains, such as plastic and rubber. Feeding activity was very low in this species: 72.5% of the specimens had empty stomachs ($f<20\%$), and only 10.0% had full foreguts ($f\geq 50\%$).

Table 3. *Geryon longipes.* Composition of diet as a function of depth and season. (*n*): no of stomachs examined. –: dietary component absent

Dietary component	Upper middle slope (n=60) %F	%N	Lower middle slope Oct.–Nov. (n=29) %F	%N	July–Oct. (n=78) %F	%N	Lower slope July–Oct. (n=17) %F	%N
Hydrozoa	6.7	2.0	3.4	1.6	6.4	2.2	5.9	2.2
Chelophyes appendiculata	6.7	2.0	3.4	1.6	6.4	2.2	–	–
Stephanoscyphus spp.	–	–	–	–	–	–	5.9	2.2
Polychaeta	23.3	7.5	–	–	52.6	18.9	47.1	17.4
Aphroditida	1.7	0.5	–	–	2.6	0.9	–	–
Hyalinoecia sp	–	–	–	–	1.3	0.4	–	–
Eunicida, unidentified	1.7	0.5	–	–	–	–	–	–
Nereidae	–	–	–	–	1.3	0.4	5.9	2.2
Sternaspidae	10.0	3.0	–	–	25.6	8.6	23.5	8.7
Serpulidae	3.3	1.0	–	–	3.8	1.3	–	–
Unidentified	8.3	2.5	3.4	1.6	21.8	7.3	17.6	6.5
Crustacea								
Decapoda								
Bathypelagic species	8.3	2.5	6.9	3.3	11.5	3.9	5.9	2.2
Sergestidae	–	–	–	–	2.6	0.9	–	–
Acanthephyra pelagica	–	–	–	–	1.3	0.4	5.9	2.2
Pasiphaea multidentata	8.3	2.5	6.9	3.3	7.7	2.6	–	–
Nectobenthic species	5.0	1.5	–	–	6.4	1.6	17.6	6.5
Plesionika sp.	3.3	1.0	–	–	–	–	–	–
Acanthephyra eximia	–	–	–	–	1.3	0.4	17.6	6.5
Pontophilus norvegicus	1.7	0.5	–	–	3.8	1.3	–	–
Unidentified	3.3	1.0	–	–	2.6	2.6	–	–
Macrura (*Calocaris macandreae*)	35.0	11.0	44.8	23.0	9.0	3.0	–	–
Anomura	10.0	3.0	13.8	6.6	1.3	0.4	–	–
Pagurus alatus	1.7	0.5	6.9	3.3	–	–	–	–
Munida tenuimana	8.3	2.5	6.9	3.3	1.3	0.4	–	–
Brachyura (*Monodaeus couchi*)	11.7	3.5	–	–	3.8	1.3	–	–
Unidentified	8.3	2.5	3.4	1.6	7.7	2.6	5.9	2.2
Euphausiacea	–	–	–	–	5.1	1.7	–	–
Mysidacea	6.7	2.5	3.4	1.6	2.6	0.9	11.8	4.3
Boreomysis arctica	6.7	2.0	3.4	1.6	2.6	0.9	5.9	2.2
Unidentified	1.7	0.5	–	–	–	–	5.9	2.2
Amphipoda								
Gammaridea	–	–	–	–	1.3	0.4	5.9	2.2
Rhachotropis sp.	–	–	–	–	1.3	0.4	–	–
Unidentified	–	–	–	–	–	–	5.9	2.2
Hyperiidea	–	–	–	–	6.4	2.1	–	–
Phrosina semilunata	–	–	–	–	5.1	1.7	–	–
Scina borealis	–	–	–	–	1.3	0.4	–	–
Isopoda	30.0	13.0	10.3	4.9	3.8	1.7	–	–
Cirolana borealis	33.3	12.0	6.9	3.3	–	–	–	–
Munnopsurus atlanticus	1.7	1.0	3.4	1.6	2.6	1.3	–	–
Ilyarachna sp.	–	–	–	–	1.3	0.4	–	–
Tanaidacea Apseudomorpha	–	–	–	–	3.8	1.3	–	–
Unidentified crustaceans	–	–	–	–	3.8	1.3	–	–
Mollusca								
Bivalvia	53.3	16.5	13.8	6.6	24.4	8.1	5.9	2.2
Taxodonta	–	–	–	–	5.1	1.7	–	–
Abra longicallus	53.3	16.5	13.8	6.6	19.2	6.0	5.9	2.2
Other Bivalvia	–	–	–	–	1.3	0.4	–	–
Gastropoda	10.0	3.5	31.0	20.3	50.0	19.4	70.6	30.4
Pteropoda	5.0	1.5	17.2	12.5	35.9	12.5	52.9	21.7
Cymbulia peroni	1.7	0.5	13.8	6.6	19.2	6.0	–	–
Opistobranchia, unidentified	–	–	–	–	–	–	11.8	4.3
Naticidae	–	–	–	–	–	–	11.8	4.3
Alvania sp.	1.7	0.5	–	–	–	–	–	–
Benthonella tenella	1.7	0.5	–	–	–	–	–	–
Other gastropoda	–	–	3.4	1.3	2.6	0.9	–	–
Prosobranchia (eggs capsules)	1.7	0.5	–	–	–	–	–	–
Cephalopoda	–	–	–	–	1.3	–	–	–
Unidentified	1.7	0.5	–	–	5.1	1.7	–	–

Table 3 (continued)

Dietary component	Upper middle slope (n = 60)		Lower middle slope				Lower slope July–Oct. (n = 17)	
			Oct.–Nov. (n = 29)		July–Oct. (n = 78)			
	%F	%N	%F	%N	%F	%N	%F	%N
Echinodermata	33.3	4.8	34.5	21.3	39.7	14.2	17.6	6.5
Echinoidea	10.0	3.0	27.6	13.1	18.0	6.0	5.9	2.2
Ophiuroidea	26.7	8.0	3.4	1.6	23.1	7.8	11.8	4.3
Holothuroidea	3.3	1.0	13.8	6.6	1.3	0.4	–	–
Molpadia musculus	3.3	1.0	6.9	3.3	–	–	–	–
Synaptidae	–	–	6.9	3.3	1.3	0.4	–	–
Sipunculoidea	8.3	3.0	–	–	1.3	0.4	–	–
Chaetognata	–	–	3.4	1.6	–	–	–	–
Osteichthyes	38.3	13.0	6.9	3.3	21.8	7.7	35.3	15.2
Cyclothone sp.	6.7	2.0	–	–	–	–	–	–
Myctophidae	6.7	2.5	–	–	–	–	–	–
Macrouridea	3.3	1.0	–	–	–	–	–	–
Unidentified	25.0	7.5	6.9	3.3	21.8	7.7	35.3	15.2
Others	1.7	0.5	6.9	3.3	2.6	0.9	17.6	6.5
Unidentified	3.3	1.0	6.9	3.3	5.1	1.7	5.9	2.2
Foraminifera	28.3		20.7		53.8		76.5	
Rhabdamina sp.	–		–		2.6		5.9	
Cyclammina sp.	–		–		2.6		–	
Robulus sp.	1.7		3.8		5.9		–	
Uvigerina sp.	8.3		–		17.9		17.6	
Ammodiscus sp.	1.7		3.4		–		–	
Pyrgo sp.	3.3		6.9		5.1		11.8	
Other benthic species	8.3		–		7.7		17.6	
Globigerinae	28.3		13.8		41.1		76.5	
Mud	5.0		–		1.3		–	
Pelagic micromollusc remains	–		–		6.4		29.4	

Trophic diversity (H') was high in the diet of *Paromola cuvieri* (4.608); 38 different food items were identified despite the low number of individuals examined. The high mean number of prey per stomach (4.4) was consistent with the high value of H'.

Geryon longipes

Principal-components analysis. The ordination of the 17 samples (Table 1) is reflected in their position relative to the first two principal axes. The first axis explained almost 17% of total variance and was related to sample depth. The deepest samples (9, 16, and 10) had the most positive scores for the first axis, and also positive scores for the second axis (Fig. 4). The second axis is more difficult to interpret. A certain amount of separation of samples as a function of season was apparent among the upper middle slope samples corresponding to autumn (Samples 1, 7, 8) and summer (Samples 2, 3, 4, 5, 6); below 1000 m no seasonal separation of samples was observed.

Diet composition on upper middle slope (550 to 750 m). During autumn (October–November) the dominant food resources (%N) were the endobenthic macruran *Calocaris macandreae*, echinoids and pteropods remains, in decreasing order of importance. The isopod *Circolana*

borealis, *Cymbulia peroni* debris, bivalves (*Abra longicallus*) and holothuroids were secondary prey items (Table 3). In terms of percentage volume (Fig. 5), *Calocaris macandreae* was the preferred prey while the echinoids *Cymbulia peroni* and *Pasiphaea multidentata* constituted less important resources.

At the same depth during summer (July), the most abundant prey items were *Calocaris macandreae*, *Cirolana borealis* and *Abra longicallus* (Table 3; Fig. 5). Less important resources were brachyuran crabs (*Monodaeus couchii*), ophiuroids and echinoids (mainly *Brissopsis lyrifera*) or unidentified fishes. Some pelagic resources were relatively abundant in the diet, for example siphonophores (*Chelophyes appendiculata*), *Pasiphaea multidentata* and mesopelagic fishes (Myctophidae, *Cyclothone* sp.).

In summary, endobenthic species (polychaetes, *Calocaris macandreae*, *Monodaeus couchii*, *Abra longicallus*, echinoderms) predominated in the diet on the upper middle slope, with epibenthic peracarids (*Cirolana borealis*) constituting a secondary resource. Seasonal variations in this depth interval were confined to a higher proportion of *Cymbulia peroni* and pteropod remains, echinoids and holothuroids in autumn.

Diet composition on lower middle slope (861 to 1250 m). No significant seasonal differences were recorded in the diet of *Geryon longipes* on the lower middle slope. The
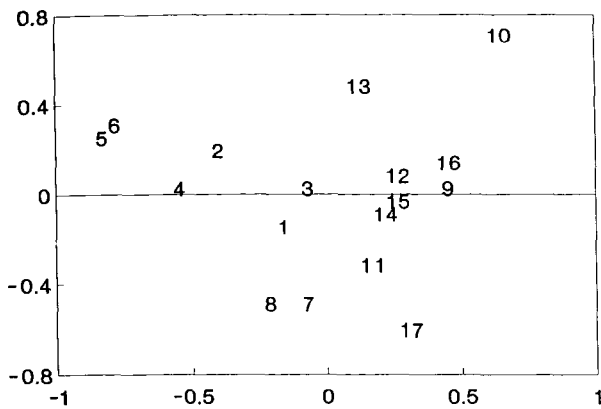
Fig. 4. *Geryon longipes*. Principal-components analysis of foregut content samples. Numbers are samples described in Table 1

high dietary overlap (similarity = 65.896) supported this. Highest %F were recorded for foraminiferans (Globigerinae, *Uvigerina* sp.). In general, the %F values were lower than for the upper middle slope samples (Table 3). The diet (%N) of *G. longipes* included polychaetes (Sternaspidae and another unidentified species), *Abra longicallus*, pteropod shells, echinoderms and fish debris. The diet was highly diversified, including *Calocaris macandreae* and other decapods (*Pontophilus norvegicus*), some peracarid crustaceans (Apseudomorpha and *Munnopsurus atlanticus*), *Cymbulia peroni* remains and plant debris. Some pelagic species also occurred in the diet; e.g. *Chelophyes appendiculata*, *Sergestes arcticus*, *Pasiphaea multidentata*, *Meganyctiphanes norvegica* and *Phrosina semilunata*. *Cymbulia peroni*, fish remains and polychaetes were the most important food items in terms of percentage volume (Fig. 5). The high volume recorded for the group "others" indicates an increasing diversification of the diet on the lower middle slope. At this depth, the proportion of benthic food items was similar to that observed for the upper middle slope, although decapods and peracarid crustaceans were less important.

Diet composition on lower slope (1300 to 1871 m). In this area, *Geryon longipes* was very scarce and only 17 specimens contained food in their foreguts; few prey items were therefore recorded (Table 3). Pteropods, fish remains and sternaspid polychaetes were the dominant prey. Foraminiferans (mainly Globigerinae) were also important at this depth. Polychaetes, *Acanthephyra* sp. and foraminiferans made up an increasing share of the diet on the lower slope on a percentage volume basis (Fig. 5).

In general, stomach fullness was very low in *Geryon longipes* (Table 4). The percentage of empty stomachs was 82.2%, while the percentage of full foreguts was only 1.5%. The high indices of dietary diversity for *G. longipes* (Table 4) largely arise from the lack of clearly dominant prey items in the diet, which led to a high equitability component for diversity. Thus, the most abundant prey, *Abra longicallus*, accounted for only 16.9% of the diet (%N). H' was higher on the lower middle slope (1000 to 1300 m) than on the upper middle slope. The low value of
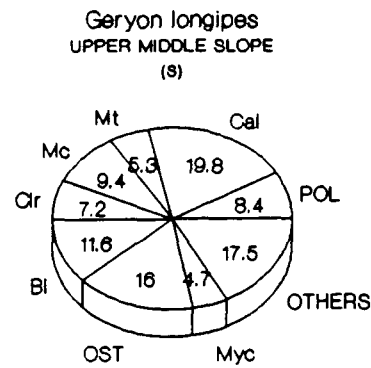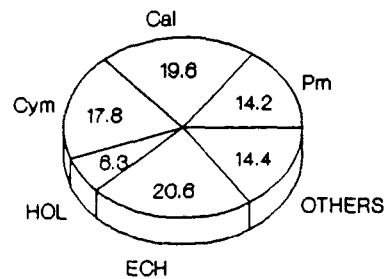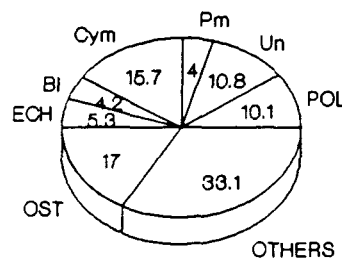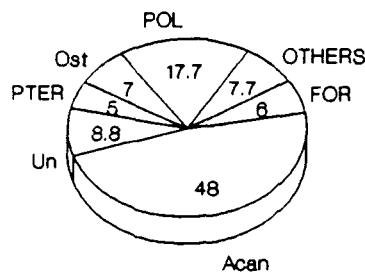

Fig. 5. *Geryon longipes*. Proportion (vol) of prey items in diet as a function of depth interval and season. POL: polychaetes; Pm: *Pasiphaea multidentata*; Ac: *Acanthephyra* sp.; Cal: *Calocaris macandreae*; Mt: *Munida tenuimana*; Mc: *Monodaeus couchi*; Cir: *Cirolana borealis*; PTER: pteropods; Cym: *Cymbulia peroni*; Bi: bivalves; CEPH: cephalopods; ECH: echinoids; HOL: holothuroids; OST: teleost fishes; Un: unidetified; FOR: foraminiferans. (A): autumn; (S): summer

Table 4. *Geryon longipes*. Stomach fullness (*f*) and trophic diversity (*H'*) as a function of depth and season

Parameter	Upper middle slope		Lower middle slope (July–Oct.)	Lower slope (July–Oct.)
	(Mar.–July)	(Oct.–Nov.)		
Stomach fullness				
No. of individuals	102	24	161	27
f < 20%	79.4%	68.6%	86.5%	84.4%
f ≥ 50%	2.0%	8.3%	3.1%	3.7%
Diversity				
No. of individuals	60	29	78	17
H'	4.302	4.009	4.653	3.827

Table 5. *Geryon longipes*. Dietary overlap (similarity index) as a function of depth and season

Slope zones	Upper middle (autumn)	Lower middle	Lower slope
Upper middle (summer)	42.696	47.901	32.282
Upper middle (autumn)	–	45.643	30.920
Lower middle	–	–	53.166

dietary diversity recorded for the lower slope was due to the small number of specimens (only 17) analyzed.

Dietary overlap was low among all the groups (Table 5) except among those below 1000 m. Finally, interspecific overlap between *Paromola cuvieri* and *Geryon longipes* on the upper middle slope was only moderate (similarity = 45.689).

Discussion

The two bathyal brachyuran crabs studied displayed highly diversified diets. The low stomach-fullness values recorded suggest that feeding frequency is very low in *Paromola cuvieri* and *Geryon longipes*. These crabs can probably survive for extended periods without food, as has been demonstrated for the astacidean *Nephrops norvegicus* (Farmer 1975). This ability may be important in enabling *P. cuvieri* and *G. longipes* to adapt to deep-bathyal zones, where trophic resources are scarce.

According to Mori (1986), *Paromola cuvieri* is a rather non-selective species that consumes a broad range of benthic resources, including non-assimilable materials (e.g. plastic remains). Scavenging on teleost fishes and sharks plays an important role in its diet, possibly as a result of commercial trawling operations (Wassenberg and Hill 1987), whereby large number of sharks (for example) are caught and subsequently discarded (own personal observations). Therefore, *P. cuvieri* should be regarded as an active scavenger (Lagardère 1976).

An important component of *Paromola cuvieri*'s diet consisted of benthic organisms of low motility (*Abra longicallus*, *Lunatia* sp., pteropod remains, foraminiferans etc.). Based on personal observations of specimens held in aquaria, *P. cuvieri* appears to be a rather slow-

moving species. It uses its chelipeds to probe the bottom, perhaps to locate buried prey (e.g. the crab *Monodaeus couchii*). The dactyli on the chelipeds bear abundant tactile setae. *P. cuvieri* also ingests material of pelagic origin (mainly *Cymbulia peroni*) that has probably settled to the bottom.

The diet of *Geryon longipes* was extremely varied and included a broad range of benthic invertebrates. *G. longipes* also appeared to ingest mobile planktonic organisms (*Chelophyes appendiculata*, *Pasiphaea multidentata*, mesopelagic fishes, etc.) dwelling near the bottom. Pelagic resources were an important yet irregular contribution to the diet. Thus, euphausiids are seasonally important in the diet of *G. longipes* (Relini Orsi and Mori 1977). The low incidence of euphausiid items recorded in the present study probably reflected the lack of samples of *G. longipes* from August–September, the period in which euphausiids are prevalent in the diet of other benthic decapods in the study area (Cartes 1991, 1993 b, Cartes and Abelló 1992).

Geryon longipes, which is a large-sized species, selects large prey items from among the macrobenthic species (Ameyaw-Akumfi and Hughes 1987). This would explain the very low incidence in its diet of the small organisms which are abundant in macrobenthic mud communities in the Catalan Sea (Reyss 1971); e.g. peracarid crustaceans (cumaceans, gammarids, etc.) and small polychaetes (glycerids, nephtyids).

Necrophagia on fishes accounted for only 5 to 10% of the diet of *Geryon longipes*. This result did not confirm the role of scavenging habits in the diet of this crab reported by Lagardère (1977). Moreover, the presence of whole remains (mandible arcs, vertebrae and otoliths) of small mesopelagic fishes in the stomachs of this geryonid crab provide evidence of some degree of predation, an aspect suggested earlier by Mori (1982).

The diets of the two deep-Mediterranean crab species showed little overlap. On the whole, the scavenging habit of *Paromola cuvieri* and the greater dependence on endobenthic prey by *Geryon longipes* differentiate the overall feeding strategies of both species. Crab-size overlap was also moderate, another factor that reduces dietary overlap (Elner 1980, Ameyaw-Akumfi and Hughes 1987).

Geryon longipes displayed high trophic diversity, close to that recorded for the penaeoidean shrimp *Aristeus an-*

tennatus (Cartes and Sardà 1989, Cartes 1991). This and the exploitation of similar prey items by the two species led Relini Orsi and Mori (1977) to suggest possible competition between both species. However, the small prey items that form the basis of the diet of *A. antennatus* (*Glycera* sp., gammarids, cumaceans) do not occur in the diet of *Geryon longipes*, and prey-size selection differs between these two species. Furthermore, Mori (1982) reported a very low feeding activity in *G. longipes*; the contents of the three fullest foreguts consisted of a single very large prey item (whole specimens of *Acanthephyra eximia* or *A. pelagica* and *Cymbulia peroni* remains). In contrast, *Aristeus antennatus* displays continuous feeding activity on a high number of small benthic invertebrates (Cartes and Sardà 1989).

Some of the preferred prey items of *Geryon longipes* on the upper middle slope (*Calocaris macandreae*, *Monodaeus couchii* and *Cirolana borealis*) were absent from its diet below 1000 m, paralleling their abundance in the environment (Cartes 1991, Cartes and Sardà 1992). The bivalve *Abra longicallus*, the holothuroid *Molpadia musculus*, and the echinoid *Brissopsis lyrifera* were not found among the middle-slope fauna below 1000 m (Carpine 1970, and own unpublished data). The absence of the preferred prey of *G. longipes* would be an important factor contributing to diversification of its diet with increasing depth, and would also explain the relatively low overlap between diets on the upper middle slope and those below 1000 m. Since only a small number of small individuals of *G. longipes* were analyzed below 1000 m, specimen size does not appear to have influenced the bathymetric trends observed in the diet. *Paromola cuvieri* consumed a broad spectrum of large benthic organisms (*Monodaeus couchii*, *Calocaris macandreae*, *Munida tenuimana*, *Cirolana borealis*, *A. longicallus*, ophiuroids), which were also far less frequent or completely absent from the environment below 1000 m depth.

On the lower middle slope, crustaceans were less important in the diet of *Geryon longipes* than at shallower depths, while pteropod remains and foraminiferans increased. Thus, the diet became poorer from the standpoint of energy intake (cf. Dauvin and Joncourt 1989) with increasing depth. This was more pronounced in the diet of *G. longipes* below 1400 m, where pteropods and foraminiferans increased. In this region, *G. longipes* behaves as a "cropper" (*sensu* Dayton and Hessler 1972). The trend towards omnivorous feeding increased with depth, as reported previously for other deep-sea invertebrates (Carey 1972, Sokolova 1972).

Below 1300 m, large endobenthic species are absent in the Catalan Sea (Cartes 1991). In general, overall macrobenthos density (Thiel 1983, Gage and Tyler 1991) and size (Jumars and Gallagher 1982, Sokolova 1990) decrease with increasing depth, as also reported for the Western Mediterranean (Chardy et al. 1973, Pérès 1985). The absence of preferential prey items and the lack of suitably sized preferred prey may contribute to the progressive decline in the density of *Paromola cuvieri* and *Geryon longipes* with increasing depth. This is similar to the situation recorded for large *Polycheles typhlops* (Cartes 1991, Cartes and Abelló 1992), and a similar ex-

planation probably holds true for the decreasing size and mean weight displayed by bathyal decapod crustacean species at depths below 1000 m in the Catalan Sea (Sardà and Cartes 1993).

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